

Gracilariopsis grevogerungii (Gracilariales, Rhodophyta), a new species of marine algae from Indonesia

Ga Hun Boo¹, Il Ki Hwang²

¹ Department of Marine Biology, Pukyong National University, Busan 48513, Republic of Korea

² Seaweed Research Institute, National Institute of Fisheries Science, Haenam 59002, Republic of Korea

Corresponding author: Ga Hun Boo (em ghboo@pknu.ac.kr ail)

Abstract

Gracilariopsis grevogerungii G.H.Boo & I.K.Hwang, **sp. nov.**, a new species from southern Indonesia, is described based on morphological features and molecular data from two genes: the plastid-encoded *rbcL* and the mitochondrial COI-5P. *Gracilariopsis grevogerungii* can be distinguished from other species in the same genus by a combination of traits: terete main axes with irregular branches and scarce short branchlets, and hemispherical cystocarps with up to 3 ostioles and 9–14 cell-layered pericarp. The species occurred on sandy-muddy substrates in the intertidal to the shallow subtidal zone. Phylogenies based on *rbcL* and COI-5P revealed its sister relationship with the subclade of *Gp. heteroclada* from China and *Gp. mclachlanii* from Tanzania. Our results highlight the need for further findings of the agar-yielding Gracilariaceae in southern Indonesia, expanding our knowledge of red algal diversity in tropical Southeast Asia.

Key words: Agar-yielding, Gracilariaceae, molecular marker, morphology, Southeast Asia



Academic editor: Ken Karol

Received: 31 March 2025

Accepted: 19 June 2025

Published: 10 July 2025

Citation: Boo GH, Hwang IK (2025) *Gracilariopsis grevogerungii* (Gracilariales, Rhodophyta), a new species of marine algae from Indonesia. PhytoKeys 259: 319–331. <https://doi.org/10.3897/phytokeys.259.154294>

Copyright: © Ga Hun Boo & Il Ki Hwang.
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

Gracilariopsis E.Y.Dawson (Gracilariaceae) is generally known as one of the major sources of agar used in food, healthcare and biotechnology industries. *Gracilariopsis* was established by Dawson (1949) to accommodate species that were previously placed in *Gracilaria* Greville and presented a small-celled, broad-based gonimoblast and the absence of nutritive filaments connecting gonimoblast with the pericarp. The established type species for the genus was *Gp. sjoestedtii* (Kylin) E.Y.Dawson. However, Papenfuss (1967) merged *Gracilariopsis* into *Gracilaria* because of the lack of morphological difference at the genus level based on observations of *Gp. sjoestedtii* and *Gracilaria verrucosa* (Hudson) Papenfuss, the generitype of *Gracilaria*. Ohmi (1958) reinstated *Gracilariopsis* based on the observation of *Gp. chorda* (Holmes) Ohmi from Japan, whereas Yamamoto (1978) included it within *Gracilaria*, despite his beautiful illustrations showing the superficial formation of spermatangia and the absence of nutritive tubular filaments in cystocarps. Fredericq and Hommersand (1989) reinstated *Gracilariopsis* including four species which have superficial spermatangia and lack nutritive tubular cells. *Gracilariopsis lemaneiformis* (Bory) Dawson, Acleto & Foldvik was designated as the generitype because of its priority over *Gp. sjoestedtii*.

Gracilariopsis has been robustly supported in phylogenies based on nuclear small subunit ribosomal DNA (SSU rDNA) and plastid *rbcL* gene sequence (Bird et al. 1994; Gurgel et al. 2003a, b). Gurgel et al. (2003b) designated the genotype of *Gracilariopsis* as *Gp. andersonii* (Grunow) Dawson, based on material from the northwest coast of America. The authors confirmed that *Gp. lemaneiformis*, for a long time considered a widespread species, is likely restricted to the Peruvian coast, and the collections of *Gp. lemaneiformis* from northwestern America correspond to *Gp. andersonii*. They also indicated that the collections of *Gp. lemaneiformis* from China and Japan may represent an undescribed species that is related to *Gp. heteroclada* J.-F.Zhang & B.-M.Xia.

The knowledge on species diversity of *Gracilariopsis* has improved with the increase of sequences availability, especially COI-5P and *rbcL* data from various regions (Bellorin et al. 2008; Gurgel et al. 2003a, b; Iyer et al. 2005; Le and Lin 2006; Lin 2008; Muangmai et al. 2014; Suzuki and Terada 2022). Recently, phylogenetic relationships of species within *Gracilariopsis* were further investigated using organellar genomes (Iha et al. 2018; Lyra et al. 2021). To date, a total of 23 species have been listed in the AlgaeBase (Guiry and Guiry 2025). Because most species of *Gracilariopsis* lack distinctive vegetative and reproductive characteristics that allow for reliable differentiation from other species (Bellorin et al. 2008), DNA sequence data is needed to evaluate the species diversity of *Gracilariopsis*.

Weber-van Bosse (1928) reported *Gracilariopsis lemaneiformis* as *Gracilaria lemaneiformis* (Bory) Greville in Indonesia, but it has not been collected since (Meinita et al. 2021). The objectives of this study were to assess the occurrence of *Gracilariopsis* species in southern Indonesia and to elucidate the taxonomic identities of the species present. During collection trips in southern Indonesia, several *Gracilariopsis*-like plants were collected from Nusa Lembongan Island, Bali. Based on detailed morphological comparisons and analyses of plastid *rbcL* and mitochondrial COI-5P sequences, we recognize these specimens as representing a new species of *Gracilariopsis*.

Materials and methods

Specimens were collected in June 2017 at Tamarind Beach (8°40'47.51"S, 115°26'10.20"E), Nusa Lembongan Island, Bali, Indonesia (Table 1). Specimens were mounted on herbarium sheets and tissue samples were dehydrated in

Table 1. Information of collection and GenBank accession number of *Gracilariopsis grevogerungii* used in the present study.

Voucher code	Collection site and date	COI-5P	<i>rbcL</i>
PKNU00672 (isotype)	Tamarind Beach, Nusa Lembongan Island, Bali, Indonesia; 8°40'47.51"S, 115°26'10.20"E; 21.vi.2017	PV106179	PV106181
PKNU00673 (holotype)	Tamarind Beach, Nusa Lembongan Island, Bali, Indonesia; 8°40'47.51"S, 115°26'10.20"E; 21.vi.2017	PV106180	PV106182
PKNU00674 (isotype)	Tamarind Beach, Nusa Lembongan Island, Bali, Indonesia; 8°40'47.51"S, 115°26'10.20"E; 21.vi.2017	PV424435	–
PKNU00676 (isotype)	Tamarind Beach, Nusa Lembongan Island, Bali, Indonesia; 8°40'47.51"S, 115°26'10.20"E; 21.vi.2017	PV424436	–

silica gels for DNA sequencing. For anatomical observation, plants were sectioned using razor blades and were stained with 1% aqueous aniline blue. Photographs were taken with a DP-71 camera (Olympus, Tokyo, Japan) mounted on a BX-51 microscope (Olympus). Vouch specimens are housed at the Herbarium of the Department of Marine Biology, Pukyong National University, Busan, Korea (**PKNU**).

DNA extraction, polymerase chain reaction amplification, and sequencing procedures followed Boo et al. (2016). The primer set used for amplifying and sequencing was F145, F754, R898, and R1442 for plastid *rbcL* (Kim et al. 2010), and GazF1 and GazR1 for mitochondrial COI-5P (Saunders 2005). All sequences were aligned together with publicly available sequences of *Gracilariopsis* species in GenBank, using the MUSCLE algorithm in MEGA7 (Kumar et al. 2016) with default parameters and the alignment was manually adjusted. *Curdiea racovitzae* Hariot, *Gracilaria vermiculophylla* (Ohmi) Papenfuss, and *Melanthalia obtusata* (Labillardiere) J.Agardh were used as outgroups based on previous studies of the Gracilariaceae (Gurgel and Fredericq 2004; Bellorin et al. 2008; Iha et al. 2018). Sequences generated in the present study were deposited in GenBank (PV106179–PV106182, PV424435, PV424436).

Phylogenies of both datasets were reconstructed using maximum likelihood (ML) and Bayesian inference (BI). The ML analysis was performed using the W-IQ-tree webserver (Trifinopoulos et al. 2016) with 1,000 ultrafast bootstrap (BS) replications (-bb 1000) and model test option (-m TEST). The BI analysis was performed with MrBayes v.3.2.1 (Ronquist et al. 2012) using the Metropolis-coupled Markov Chain Monte Carlo (MC3) with the best-fitting substitution model selected by IQ-tree. Four million generations of two independent runs were performed with four chains and sampling trees every 100 generations. The burn-in period was identified graphically by tracking the likelihoods at each generation to determine whether they reached a plateau. Twenty-five percent of saved trees were removed, and the remaining trees were used to infer Bayesian posterior probabilities (BPP).

Results

Molecular phylogeny

Six sequences were generated in the present study, two *rbcL* and four COI-5P sequences. A total of 25 *rbcL* sequences were aligned, including 23 publicly available sequences of *Gracilariopsis* and three outgroups. In the *rbcL* phylogeny (Fig. 1), the Indonesian taxon was distinct from the other species in the genus, and formed a sister relationship with the clade of *Gp. heteroclada*, *Gp. irregularis* (I.A.Abbott) N.Muangmai, A.Chirapart & A.Lewmanomont, and *Gp. mclachlanii* Buriyo, Bellorin & M.C.Oliveira (98% MLBS, 1.0 BPP). The pairwise divergence of *rbcL* sequences between the Indonesian taxon and related species was 2.6–3.3%, with identical sequences among the Indonesian specimens.

In the COI-5P phylogeny (Fig. 2), the Indonesian taxon placed in a position largely congruent with that in the *rbcL* phylogeny, forming a clade with *Gp. heteroclada* and *Gp. mclachlanii* (100% MLBS, 1.0 BPP). The pairwise divergence of COI-5P sequences between the Indonesian taxon and related species was 4.7–6.1%, with identical sequences among the Indonesian specimens.

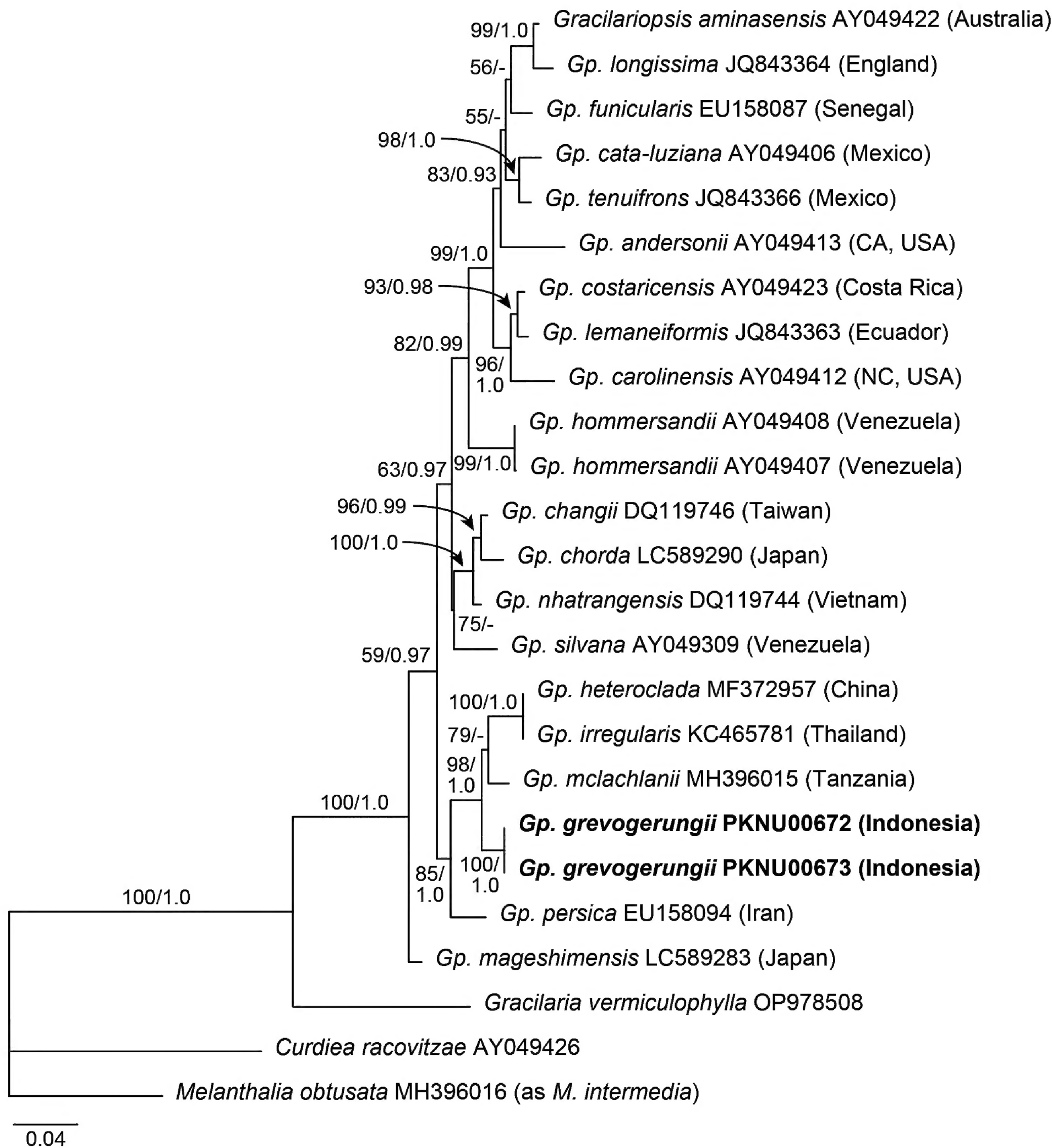


Figure 1. Maximum likelihood (ML) phylogeny of *Gracilariopsis* using plastid *rbcL* sequences. ML bootstrap values ($\geq 50\%$) and Bayesian posterior probabilities (≥ 0.9) are shown at branches. Bold letters indicate *Gp. grevogerungii* sp. nov.

Morphological observations

Details of morphological features are introduced in description and illustration below (Figs 3, 4). The *Gracilariopsis* species from Indonesia is characteristic of the genus in the absence of nutritive tubular cells between the gonimoblast and pericarp. The species can be distinguished from other species of *Gracilariopsis* by a combination of terete main axes with irregular branches with sparse, filiform branchlets (up to 4 mm), scattered tetrasporangia on axes and branches, and hemispherical cystocarps with up to 3 ostioles and 9–14 cell-layered

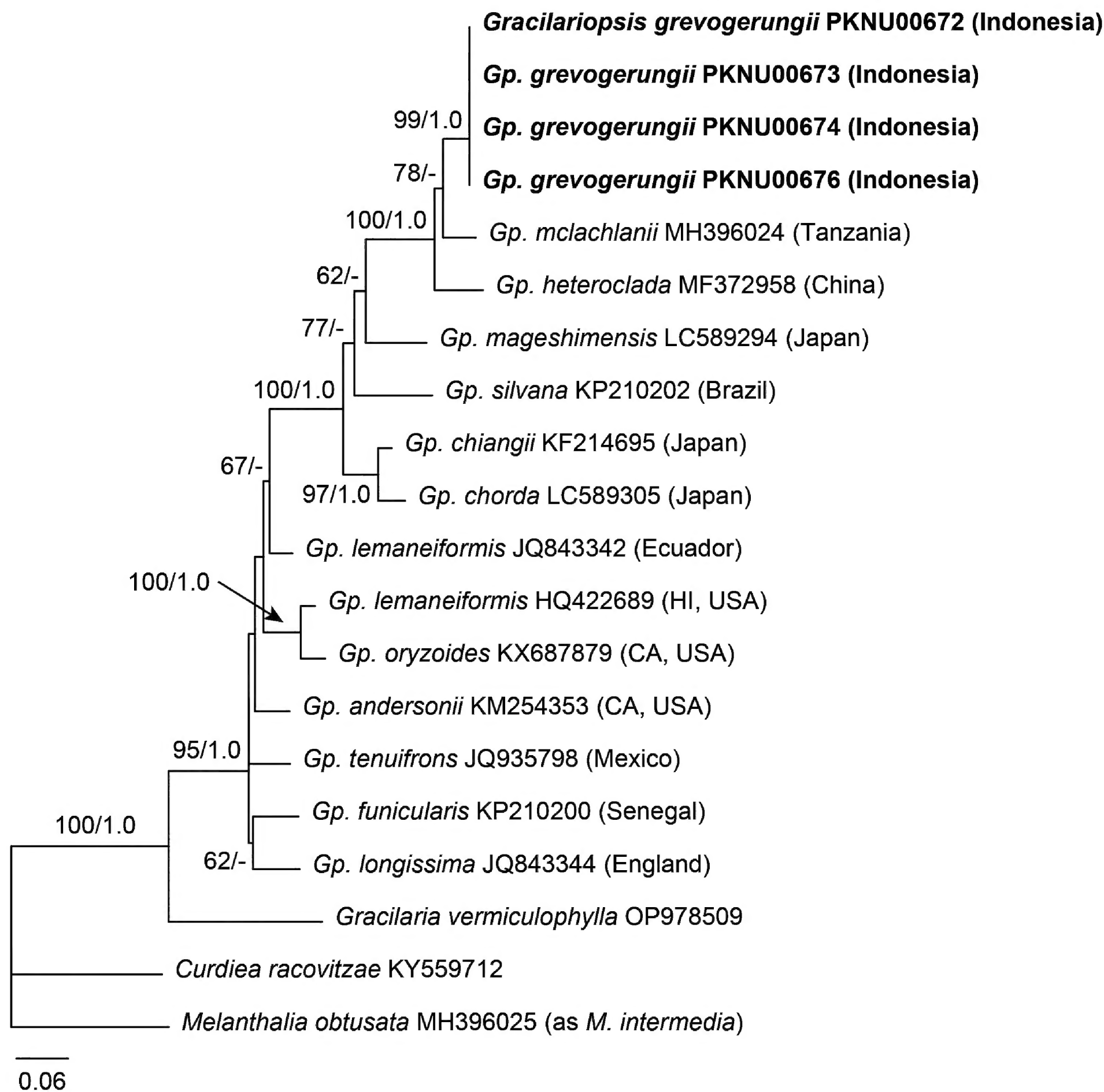


Figure 2. Maximum likelihood (ML) phylogeny of *Gracilariopsis* using mitochondrial COI-5P sequences. ML bootstrap values ($\geq 50\%$) and Bayesian posterior probabilities (≥ 0.9) are shown at branches. Bold letters indicate *Gp. grevogerungii* sp. nov.

pericarps. A morphological comparison of Indonesian *Gracilariopsis* with other terete species of the genus is given in Table 2. However, without DNA sequences, it is difficult to recognize the Indonesian *Gracilariopsis*.

***Gracilariopsis grevogerungii* G.H.Boo & I.K.Hwang, sp. nov.**

Figs 3, 4

Description. Thallus up to 13 cm tall, solitary, yellow-green to pale red in color. Main axes cylindrical throughout, about 640 μm in diameter, arising from a small disk-like holdfast (Fig. 3). Indeterminate branches often unbranched at the base, scattered, alternate to irregularly arising to 1–2 orders, slightly constricted at

Table 2. Morphology and distribution of *Gracilariopsis grevogerungii* and similar species.

	<i>Gp. grevogerungii</i> G.H.Boo & I.K.Hwang, sp. nov.	<i>Gp. chiangii</i> Showe M.Lin 2008	<i>Gp. chorda</i> (Holmes) Ohmi 1958	<i>Gp. heteroclada</i> J.-F. Zhang & B.-M.Xia 1991	<i>Gp. irregularis</i> (Abbott) Muangmai, Chirapat & Lewmanomont, 2014	<i>Gp. mclachlanii</i> Buriyo, Bellorin & M.C.Oliveira in Bellorin et al. 2008	<i>Gp. nhatrangensis</i> Nhu Hau Le & Showe M.Lin 2006
Type locality	Tamarind Beach, Lembongan Island, Bali, Indonesia	Wu-Shih-Bi Harbor, Tou-Cheng Township, Taiwan	Enoura, Namazu city, Shizuoka Pref., Japan	Yinggehai, Hainan, Guangdong, China	Ao Len, Trat Peninsula, Thailand	Nungwi Marani, Unguja Island, Zanzibar, Tanzania	Cua Be, Nha Trang, Southern Vietnam
Thallus length	up to 13 cm	up to 22 cm	up to 200 cm	up to 70 cm	up to 10 cm	>150 cm	up to 18 cm
Main axes	percurrent, terete, 640 µm in diam.	terete, 3 mm in diam., up to 8 main axes arising from a holdfast	more or less percurrent, cylindrical, compressed, up to 5 mm in diam.	percurrent or not, cylindrical, up to 3 mm in diam.	percurrent, cylindrical, 2–2.5 mm in diam.	percurrent or not, cylindrical throughout, 1–3 mm in diam.	cylindrical to terete, up to 2.2 mm in diam., up to 15 main axes arising from a holdfast
Indeterminate branches	sparsely irregular	5–7 densely clustered in the middle of axes, regenerating branches at the tip	alternate or irregular, long	long, up to four orders, easily broken, irregularly alternate, secund or furcate	very irregular to secund, sometimes inflated in middle, up to third orders	unbranched at the base, scattered, alternate to irregular, up to four orders	branched 1–2 orders from the base
Determinate branches	filiform, up to 5 mm long, scarce, irregular	absent	filiform, absent in young thalli, but often numerous, short	short, spinose, gradually tapered, non-constricted at the base	short, sometimes spine-like, frequently crowded	absent	numerous, racemose
Cortex	1–2 layers of small cells	up to 3 layers of ovoid cells	up to 3 layers of globular cells with dense cytoplasm, with the subcortex of 3–4 layers of elongated cells	2–3 layers of small, roundish cells	1–2 layers of cortical cells	2 layers of isodiametric to elongate cells, with the subcortex of 1–3 layers	3–4 layers of ovoid cells, 6–7 µm in diam., with the subcortex of 1–3 layers
Medulla	large, thin-walled cells	large thin-walled cells	5–7 layers of large, polygonal to spherical, vacuolated cells	large, parenchymatous cells	5–12 cell layers	Large globose cells, thin-walled, highly vacuolated	large, thin-walled, vacuolated cells
Cystocarp	hemispherical, scattered on main axes or branches	dome-shaped, broad-based, carposporangia in branched chains	slightly beaked, constricted at bases	prominently protruding or subconical, around 1,000 µm in diam., non- constricted at the base	dome-shaped, not constricted, 200 µm in diam.	prominent, not constricted at the base	prominent, not constricted at the base
Pericarp	9–14 cell layers	10–14 cell layers	6–8 cell layers	7–8 cell layers	10–12 cell layers	8–13 cell layers	11–17 cell layers
Spermantangia	not found	not found	scattered, continuous over branch surface	scattered, continuous over branch surface	continuous or discontinuous cluster	scattered, irregular pale patches	superficial
Tetrasporangia	scattered, cruciate, 20–34 × 19–24 µm in size	scattered, cruciate, 40–50 × 25–30 µm in size	scattered on surface, cruciate, 46–56 × 26– 35 µm in size	scattered, cruciate to irregularly tetrahedral, 33–36 × 16–26 µm in size	cruciate, 28–35 µm in diam.	scattered, decussate to cruciate, 20–60 × 15–32 µm in size	cruciate, 20–30 × 10–20 µm in size
Distribution	Southern Indonesia	Taiwan, Japan	China, Japan, Korea	China, Malaysia, Philippines	Thailand	Tanzania	Vietnam
Reference	This study	Lin 2008; Yang and Kim 2015	Yamamoto 1978; Kim et al. 2008	Zhang and Xia 1988; Hurtado-Ponce and Liao 1998; Yang and Kim 2015	Abbott 1988; Muangmai et al. 2014	Bellorin et al. 2008	Le and Lin 2006

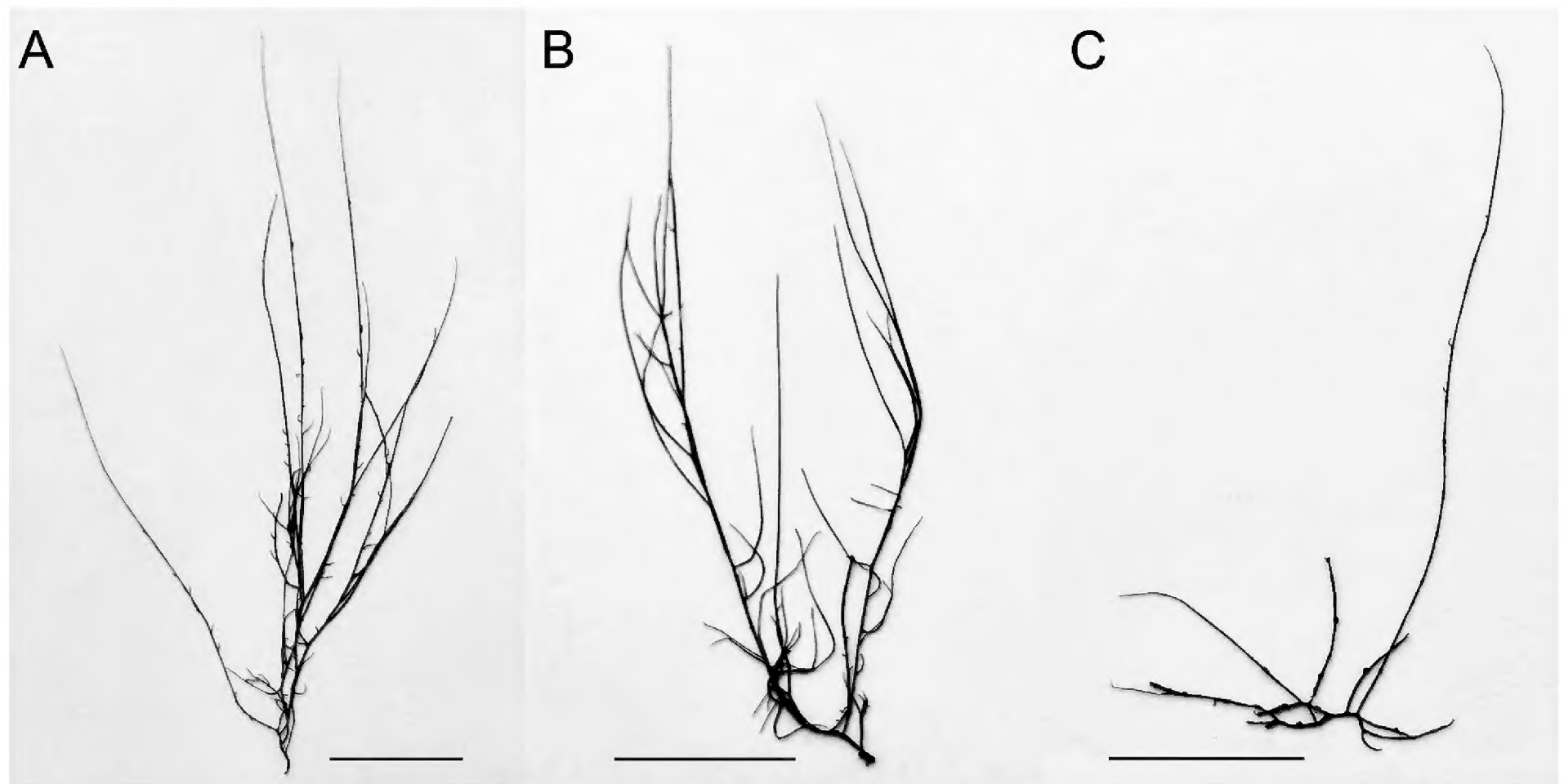


Figure 3. A–C. Habit of *Gracilariopsis grevogerungii* sp. nov. **A.** Holotype specimen (PKNU00673) from Tamarind Beach, Nusa Lembongan Island, Bali, Indonesia; 21 June, 2017; **B.** Isotype specimen having tetrasporangia (PKNU00676); **C.** Isotype specimen bearing cystocarps (PKNU00672). Scale bars: 2 cm (**A–C**).

the base and tapering gradually toward apices. Determinate branches up to 4 mm long, irregularly alternate or scattered. Cortices composed of two to three layers of small isodiametric or anticlinally elongate cells (Fig. 4A, B), measuring $3.2\text{--}6.4 \times 7.5\text{--}12.8 \mu\text{m}$ in size, with dense content, heavily pigmented, connected only with their parental cells by primary pit connections. Medulla composed of large globose cells, $114\text{--}163 \mu\text{m}$ in diameter in transverse sections, thick-walled and highly vacuolated, lacking pigments. Transition in cell size from cortex to medulla abrupt (Fig. 4C). Large basal cells of deciduous hairs frequently occurring near the surface. Cystocarps $492\text{--}805 \mu\text{m}$ in diameter and $689\text{--}884 \mu\text{m}$ in height, hemispherical, scattered on main axes or determinate branches, slightly constricted at the base. Cystocarps slightly constricted at the base, with up to three ostioles (Fig. 4D, E). Carposporangia initials formed in long chains and radially elongated (Fig. 4F, G). Two gonimoblasts formed in a single cystocarp (Fig. 4H). Mature cystocarps released carpospores through ostioles (Fig. 4I). Pericarps about $115 \mu\text{m}$ thick, formed by 9–14 cell layers. Tetrasporangia embedded in the cortex (Fig. 4J). Tetrasporangial initials formed from inner cortical cells (Fig. 4K). Tetrasporangia decussately or cruciately divided, ovoid, $20\text{--}34 \times 19\text{--}24 \mu\text{m}$ in size (Fig. 4L, M).

Diagnosis. Diagnosed by a combination of characters: simple terete axes with irregular long branches and scarce short branchlets, hemispherical cystocarps with up to 3 ostioles, 9–14 cell-layered pericarp, and DNA sequences (accession number: PV106182 for *rbcL* and PV106180 for *COI-5P*).

Type. INDONESIA • Bali, Nusa Lembongan Island, Tamarind Beach, $8^{\circ}40'47.51''\text{S}$, $115^{\circ}26'10.20''\text{E}$, 21 Jun. 2017, collected by Sung Min Boo without collection numbers (Holotype: PKNU00673!; Isotypes: PKNU00672!, PKNU00674!, and PKNU00676!; Paratype: PKNU00675!). Types are deposited in the herbarium of the Department of Marine Biology, Pukyong National University, Busan, Korea (PKNU).

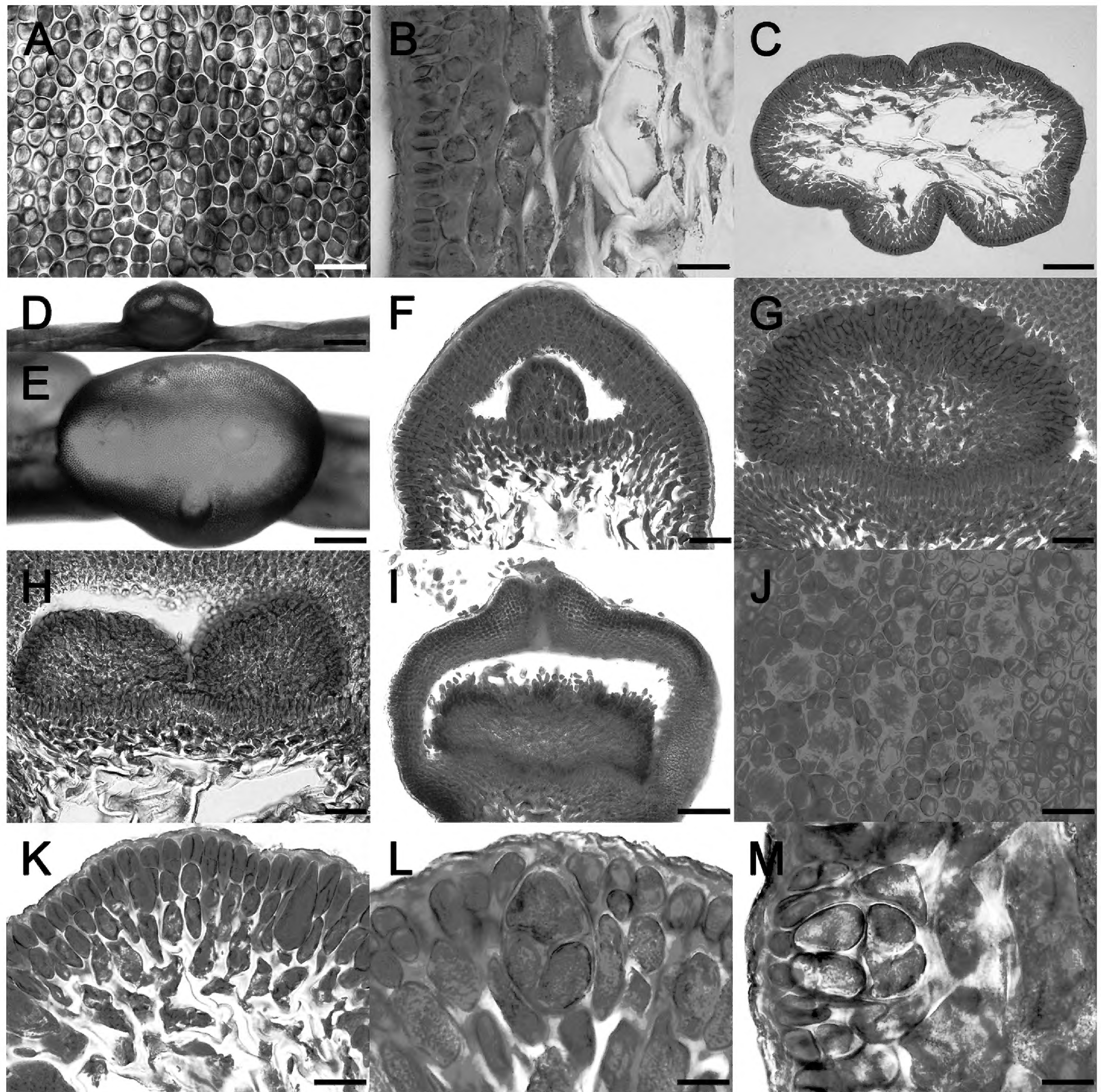


Figure 4. A–M. Morphology and anatomy of *Gracilariopsis grevogerungii* sp. nov. **A.** Surface view of axis showing irregularly arranged cortical cells; **B.** Longitudinal section of axis showing compact cortex and medulla; **C.** Transverse section of axis showing abrupt transition in cells size from cortex to medulla; **D.** Hemispherical cystocarp; **E.** Three ostioles on a single cystocarp; **F.** Longitudinal section of cystocarp showing early stage of gonimoblast; **G.** Longitudinal section of cystocarp lacking nutritive tubular cells between gonimoblast and pericarp; **H.** Two gonimoblasts sometimes formed within a single cystocarp; **I.** Longitudinal section of cystocarp showing releasing carpospores through ostiole; **J.** Tetrasporangia partially immersed by cortical cells; **K.** Tetrasporangial initial formed from inner cortical cells; **L, M.** Decussately to cruciately divided tetrasporangia. Scale bars: 20 μm (**A, B, J–M**); 100 μm (**C, I**); 400 μm (**D**); 200 μm (**E**); 40 μm (**F–H**).

Habitat and distribution. *Gracilariopsis grevogerungii* grows on intertidal to shallow subtidal sandy-muddy substrates. It is currently demonstrated in the type locality solely using DNA sequences, but its range is likely expanded to the surrounding waters with additional collections (see Discussion).

Etymology. Species epithet is given in honor of Dr Grevo Soleman Gerung for his contributions to the knowledge of seaweed diversity in Indonesia.

Discussion

Gracilariopsis grevogerungii is the only described southern Indonesian species of *Gracilariopsis* investigated by both *rbcL* and COI-5P sequences, as well as morphology. The cystocarp anatomy revealed the chains of carposporangia and the lack of nutritive tubular cells, typical characters of *Gracilariopsis*. *Gracilariopsis grevogerungii* was likely misidentified as *Gp. lemaneiformis* based on specimens collected in Flores Island and Tanah Djampea, Indonesia (Weber-van Bosse 1928). Its illustration of cystocarp having 10–17 cell layers in pericarp and lacking the nutritive tubular cells matches well with *Gp. grevogerungii*.

Gracilariopsis grevogerungii has likely been misidentified as terete species of *Gracilaria*. For example, during the present study, *Gracilaria edulis* (S.G.Gmelin) P.C.Silva was collected in Benoa Bay, Bali, very close to Nasa Lembongan Island. It is a common species in Indonesia and also included in the export list of Indonesian hydrocolloid seaweeds (Meinita et al. 2021; Basyuni et al. 2024). However, COI-5P sequences from our collections of *G. edulis* (GHB, unpubl.) revealed its difference from *Gp. grevogerungii*. Again, *Gracilaria* is well segregated from *Gracilariopsis* by the presence of nutritive filaments in the cystocarp and by molecular data (Gurgel et al. 2003b; Bellorin et al. 2008).

Gracilariopsis sp. from Zamboanga city, Philippines, which lacks fine, determinate branchlets (Hurtado-Ponce and Liao 1998), is morphologically similar to *Gp. grevogerungii*. DNA sequences from the Philippine collection are necessary to confirm its identity. *Gracilariopsis lemaneiformis* has still been reported in China (Wang et al. 2023), even though it has been confirmed by *rbcL* sequences that the Chinese specimens do not correspond to *Gp. lemaneiformis* (whose type locality is in Peru), but to *Gp. chorda* (whose type locality is in Japan). Additional sampling at sand-muddy coastal regions will likely extend the range of *Gp. grevogerungii* into other locations in Indonesia or surrounding waters.

Two species of *Gracilariopsis* were closely related to *Gp. grevogerungii* in both *rbcL* and COI-5P phylogenies. *Gracilariopsis mclachlanii*, originally described for Tanzanian specimens, is recognized by large cylindrical form of thallus, 8–13 cell layers of pericarp, and cleavage of spermatangia from spermatangial mother cells through concavo-convex oblique septa (Bellorin et al. 2008). *Gracilariopsis heteroclada*, first described for Chinese specimens, is characterized by slender, filiform indeterminate branches that arise alternatively and are beset with fine, regularly-disposed determinate branchlets (Zhang and Xia 1988; Hurtado-Ponce and Liao 1998).

Several species of *Gracilariopsis*, including *Gp. heteroclada*, have been previously recognized in Southeast Asia (Pham 1969; Le and Lin 2006; Lin 2008; Muangmai et al. 2014). Most species except foliose *Gp. mageshimensis* Mas. Suzuki & R.Terada from Japan resemble *Gp. grevogerungii* in their habits with filiform thalli having irregular lateral branches from main axes (Table 2). Of these, *Gp. chiangii* Showe M.Lin, *Gp. heteroclada*, and *Gp. nhatrangensis* Nhu Hau Le & Showe M.Lin have been well delimited by DNA sequences and morphology (Le and Lin 2006; Lin 2008; Wang et al. 2023). *Gracilariopsis chiangii* is characterized by small-sized thallus (15–22 cm in length) and 1–2(–3) orders of branches from the base to middle part of thallus (Lin 2008). *Gracilariopsis nhatrangensis* is characterized by 1–15 main branches (up to 18 cm tall), arising from a discoid holdfast and numerous, racemose branchlets on main axes (Le and Lin 2006).

Gracilariopsis irregularis from Thailand is distinguished by having short (up to 10 cm) and succulent axes with an irregular secondary branching pattern (Muangmai et al. 2014). However, *Gp. irregularis* requires reexamination by COI-5P and other molecular markers because of its homogeneity to *Gp. heteroclada* in *rbcL*. It is important to reexamine the holotypes or topotype materials of two Vietnamese species, *Gp. nganii* Pham and *Gp. phanthiens* Pham, which have not been recorded since the original publication (Le and Lin 2006; Pham 1969), to elucidate their relationships with *Gp. grevogerungii* and other *Gracilariopsis* species. Because most *Gracilariopsis* species have similar vegetative traits (Bellorin et al. 2008), it is difficult to discriminate *Gp. grevogerungii* from other cylindrical species of *Gracilariopsis* in Southeast Asia without DNA sequences.

Conclusions

DNA sequence analyses were essential for the recognition of a new tropical species, *Gracilariopsis grevogerungii*, from southern Indonesia. This study highlights the critical role of molecular data in elucidating the biodiversity of a morphologically simple group of marine red algae. *Gracilariopsis grevogerungii*, along with *Gracilaria* species, is expected to be included in the export list of Indonesian hydrocolloid seaweeds. Our integrative taxonomy, combining molecular and morphological evidence, contributes to the clarification of commercial seaweed species and the cataloguing of red algal biodiversity. This study emphasizes the necessity for continued taxonomic and molecular investigations of the agar-producing genus *Gracilariopsis* in Indonesia and adjacent regions.

Acknowledgements

We thank Grevo Soleman Gerung for his information on collection locality and Sung Min Boo for his permission of specimens.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

Funding

This study was supported by the National Research Foundation of Korea (NRF) grant funded by the Korea government (MSIT) (RS-2025-00521216) and the National Institute of Fisheries Science, Ministry of Oceans and Fisheries, Korea (R2025025).

Author contributions

Conceptualization: GHB. DNA sequencing and analysis: GHB. Morphological observations: IKH, GHB. Writing – original draft: GHB, IKH. Writing – review and editing: GHB, IKH.

Author ORCIDs

Ga Hun Boo  <https://orcid.org/0000-0002-3019-2678>

Il Ki Hwang  <https://orcid.org/0009-0005-5120-0891>

Data availability

All of the data that support the findings of this study are available in the main text.

References

- Abbott IA (1988) Some species of *Gracilaria* and *Polycavernosa* from Thailand. In: Abbott IA (Ed.) Taxonomy of Economic Seaweeds with Reference to Some Pacific and Caribbean Species (Vol. II). California Sea Grant College Program, La Jolla, 137–150.
- Basyuni M, Puspita M, Rahmania R, Albasri H, Pratama I, Purbani D, Aznawi AA, Mubaraq A, Al Mustaniroh SS, Menne F, Rahmila YI, Salmo III SG, Susilowati A, Larekeng SH, Ardli E, Kajita T (2024) Current biodiversity status, distribution, and prospects of seaweed in Indonesia: A systematic review. *Heliyon* 10: e31073. <https://doi.org/10.1016/j.heliyon.2024.e31073>
- Bellorin AM, Buriyo A, Sohrabipour J, Oliveira MC, Oliveira EC (2008) *Gracilariopsis mclachlanii* sp. nov. and *Gracilariopsis persica* sp. nov. of the Gracilariaceae (Gracilariales, Rhodophyta) from the Indian Ocean. *Journal of Phycology* 44: 1022–1032. <https://doi.org/10.1111/j.1529-8817.2008.00552.x>
- Bird CJ, Ragan MA, Crichley AT, Rice EL, Gutell RR (1994) Molecular relationships among Gracilariaceae (Rhodophyta): Further observations on some undetermined species. *European Journal of Phycology* 29: 195–202. <https://doi.org/10.1080/09670269400650641>
- Boo GH, Le Gall L, Miller KA, Freshwater DW, Wernberg T, Terada R, Yoon KJ, Boo SM (2016) A novel phylogeny of the Gelidiales (Rhodophyta) based on five genes including nuclear *CesA*, with descriptions of *Orthogonacladia* gen. nov. and Orthogonacladiaceae fam. nov. *Molecular Phylogenetics and Evolution* 101: 359–372. <https://doi.org/10.1016/j.ympev.2016.05.018>
- Dawson EY (1949) Studies of the northeast Pacific Gracilariaceae. *Occasional Papers of the Allan Hancock Foundation* 7: 1–105.
- Fredericq S, Hommersand MH (1989) Comparative morphology and taxonomic status of *Gracilariopsis* (Gracilariales, Rhodophyta). *Journal of Phycology* 25: 228–241. <https://doi.org/10.1111/j.1529-8817.1989.tb00117.x>
- Guiry MD, Guiry GM (2025) *AlgaeBase*. World-wide electronic publication, National University of Ireland, Galway. <https://www.algaebase.org/> [accessed 5 January 2025]
- Gurgel CFD, Fredericq S (2004) Systematics of the Gracilariaceae (Gracilariales, Rhodophyta): A critical assessment based on *rbcL* sequence analysis. *Journal of Phycology* 40: 138–159. <https://doi.org/10.1111/j.0022-3646.2003.02-129.x>
- Gurgel CFD, Fredericq S, Norris JN (2003a) *Gracilariopsis silvana* sp. nov., *G. hommersandii* sp. nov., and *G. cata-luziana* sp. nov., three new species of Gracilariaceae (Gracilariales, Rhodophyta) from the western Atlantic. *Hidrobiológica* 13: 57–68.
- Gurgel CFD, Liao LM, Fredericq S, Hommersand MH (2003b) Systematics of *Gracilariopsis* (Gracilariales, Rhodophyta) based on *rbcL* sequence analyses and morphological evidence. *Journal of Phycology* 39: 154–171. <https://doi.org/10.1046/j.1529-8817.2003.02046.x>
- Hurtado-Ponce AQ, Liao LM (1998) The genus *Gracilariopsis* (Rhodophyta, Gracilariales) in the Philippines: morphological and taxonomic confirmations. *The Philippine Scientist* 35: 141–151. <http://hdl.handle.net/10862/2135>

- Iha C, Grassa CJ, Lyra GdM, Davis CC, Verbruggen H, Oliveira MC (2018) Organellar genomics: A useful tool to study evolutionary relationships and molecular evolution in Gracilariaceae (Rhodophyta). *Journal of Phycology* 54: 775–787. <https://doi.org/10.1111/jpy.12765>
- Iyer R, Tronchin EM, Bolton JJ, Coyne VE (2005) Molecular systematics of the Gracilariaceae (Gracilariales, Rhodophyta) with emphasis on southern Africa. *Journal of Phycology* 41: 672–684. <https://doi.org/10.1111/j.1529-8817.2005.00088.x>
- Kim MS, Yang EC, Kim SY, Hwang IK, Boo SM (2008) Reinstatement of *Gracilariopsis chorda* (Gracilariaceae, Rhodophyta) based on plastid *rbcL* and mitochondrial *cox1* sequences. *Algae – Korean Phycological Society* 23: 209–217. <https://doi.org/10.4490/ALGAE.2008.23.3.209>
- Kim MS, Kim SY, Nelson W (2010) *Symphyclocladia lithophila* sp. nov. (Rhodomelaceae, Ceramiales), a new Korean red algal species based on morphology and *rbcL* sequences. *Botanica Marina* 53: 233–241. <https://doi.org/10.1515/BOT.2010.031>
- Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33: 1870–1874. <https://doi.org/10.1093/molbev/msw054>
- Le NH, Lin SM (2006) *Gracilariopsis nhatrangensis* (Gracilariaceae, Rhodophyta), a new marine red alga from Nhatrang, southern Vietnam. *Botanical Studies* 47: 329–337.
- Lin S-M (2008) Morphological and phylogenetic studies of *Gracilariopsis chiangii*, new species (Gracilariaceae, Rhodophyta), an alga presently known as *Gracilaria chorda* in Taiwan. *The Raffles Bulletin of Zoology* 19(Supplement): 19–26.
- Lyra GDM, Iha C, Grassa CJ, Cai L, Zhang HG, Lane C, Blouin N, Oliveira MC, Nunes JMDC, Davis CC (2021) Phylogenomics, divergence time estimation and trait evolution provide a new look into the Gracilariales (Rhodophyta). *Molecular Phylogenetics and Evolution* 165: e107294. <https://doi.org/10.1016/j.ympev.2021.107294>
- Meinita MDN, Akromah N, Andriyani N, Setijanto, Harwanto D, Liu T (2021) Molecular identification of *Gracilaria* species (Gracilariales, Rhodophyta) obtained from the South Coast of Java Island, Indonesia. *Biodiversitas* 22: 3046–3056. <https://doi.org/10.13057/biodiv/d220759>
- Muangmai N, Yamagishi Y, Zuccarello GC, Chirapart A, Lewmanomont K (2014) Transferring *Gracilaria irregularis* (Gracilariaceae, Rhodophyta) from Thailand to *Gracilariopsis* based on morphological and molecular analyses. *Phycological Research* 62: 29–35. <https://doi.org/10.1111/pre.12032>
- Ohmi H (1958) The species of *Gracilaria* and *Gracilariopsis* from Japan and adjacent waters. *Memoirs of the Faculty of Fisheries, Hokkaido University* 6: 1–66.
- Papenfuss GF (1967) Notes on algal nomenclature–V. various Chlorophyceae and Rhodophyceae. *Phykos (Algiers)* 5: 95–103.
- Pham HH (1969) Marine Algae of South Vietnam (Rong biển Việt Nam). Sai Gon Study Center, Ministry of Education and Youth, 558 pp.
- Ronquist F, Teslenko M, van Der Mark P, Ayres D, Darling A, Hohna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Saunders GW (2005) Applying DNA barcoding to red macroalgae: A preliminary appraisal holds promise for future applications. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 360: 1879–1888. <https://doi.org/10.1098/rstb.2005.1719>

- Suzuki M, Terada R (2022) A new flattened species of *Gracilariopsis* (Gracilariales, Rhodophyta) from Japan. *Phycologia* 60: 158–163. <https://doi.org/10.1080/00318884.2021.1880755>
- Trifinopoulos J, Nguyen L-T, von Haeseler A, Minh BQ (2016) W-IQ-TREE: A fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research* 44: W232–W235. <https://doi.org/10.1093/nar/gkw256>
- Wang X, Guo M, Yan S, Wang Y, Sun Z, Xia B, Wang G (2023) Diversity of Gracilariaceae (Rhodophyta) in China: An integrative morphological and molecular assessment including a description of *Gracilaria tsengii* sp. nov. *Algal Research* 71: e103074. <https://doi.org/10.1016/j.algal.2023.103074>
- Weber-van Bosse A (1928) Liste des algues du Siboga, IV. Rhodophyceae, Part 3. Gigartinales et Rhodymeniales. *Siboga-Expeditie Monographie* 59d: 393–533.
- Yamamoto H (1978) Systematic and anatomical study of the genus *Gracilaria* in Japan. *Memoirs of the Faculty of Fisheries, Hokkaido University* 25: 97–152.
- Yang MY, Kim MS (2015) Molecular analyses for identification of the Gracilariaceae (Rhodophyta) from the Asia-Pacific region. *Genes & Genomics* 37: 775–787. <https://doi.org/10.1007/s13258-015-0306-1>
- Zhang J, Xia B-M (1988) On two new *Gracilaria* (Gigartinales, Rhodophyta) from South China. In: Abbott IA (Ed.) *Taxonomy of Economic Seaweeds with Reference to Some Pacific and Caribbean Species (Vol. II)*. California Sea Grant College Program, La Jolla, 131–136.